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PATTERNS OF SPACE USE IN GRASSLAND BIRD COMMUNITIES DURING WINTER

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Spatial relations of birds are the result of responses by individuals to various features of the environment (Brown and Orians 1970). Specific environmental features, such as nesting or roosting sites, or the amount of cover, can influence the use of space by individuals (Davis 1973, Post 1974, Snapp 1976, Pulliam and Mills 1977). Space use patterns often reflect the abilities of birds to defend and locate food or other resources (Stenger 1958, Cody 1971, Schoener 1971, Krebs 1973), avoid predation (Pulliam 1973, Bertram 1978, Kenward 1978), and interact with other individuals (Krebs 1971, Myers et al. 1979). Flocking may simultaneously enhance food exploitation and predator detection (Pulliam 1973, Powell 1974). However, Goss-Custard (1970) and Caraco (1979) pointed out that group membership may have disadvantages, such as increasing susceptibility to disease or parasites, foraging interference, and increasing costs associated with intraspecific aggression. Thus, space-use patterns of birds reflect a balance of selective forces acting both to draw organisms together and spread them apart.

This paper describes the various types of spatial occupancy used by passerine birds in open grasslands during winter, and assesses some potential mechanisms influencing these spatial relations. Grassland habitats provide a relatively simple homogeneous setting compared to scrub and woodland habitats in which factors affecting extremes in space use can simultaneously be assessed. Granivory is the primary foraging mode of grassland birds during winter (Pulliam 1975), further simplifying the system. Climatic severity and reduced winter daylength necessitate effective exploitation of food resources. While most passerines are territorial during the breeding season, the constraints of reproduction are not present during winter.

METHODS

Grasslands of varied grazing pressure or cultivation practices in several regions of Oklahoma and Texas were used. Data were collected at 14 sites from the winters of 1975–76 through 1978–79. The sampling period began 15 November and ended 15 February for each season. One Oklahoma site was also sampled in January and February 1975. The sites included seven in central Oklahoma (Cleveland, Grady, and McClain counties), three in western Texas (Muleshoe National Wildlife Refuge, Bailey County), and four on the Rob and Bessie Welder Wildlife Refuge (San Patricio County) in southern coastal Texas. The sizes of sites ranged from about 30 ha on the smallest sites in southern Texas to greater than 100 ha. Sites were characterized by their uniformity and large size, thus minimizing edge effect with other habitats. Two of the southern Texas sites contained about 5% shrub cover. Otherwise tree or shrub cover were absent or comprised less than 0.5% cover, consisting of isolated individual plants less than 3 m in height.

Sites were classified on the basis of grazing pressure or cultivation practices. A site was considered a lightly grazed grassland (LG) when the dominant palatable grasses had uniformly grown to heights approaching their maximum potential heights. For LGs in Oklahoma and southern Texas, maximum vegetation heights ranged from 1–2 m. In western Texas, maximum grass heights of LGs were about 0.5 m. When dominant palatable grasses occurred in distinct clumps, the site was designated a moderately grazed grassland (MG). Vegetation heights of MGs were up to 1 m in Oklahoma, and 1.5 m in southern Texas. When the dominant palatable grasses were absent, or present only in widely scattered clumps and/or grazed to near ground level, the site was considered a heavily grazed grassland (HG). Vegetation heights in HGs were less than 0.5 m on all sites. The cultivated sites were planted with winter wheat (*Triticum aestivum*); these sites had been harvested of a sorghum (*Sorghum bicolor*) crop in fall. On one cultivated site, only the heads of the sorghum were removed: the field was left fallow in this condition for the winter observation period. More detailed site descriptions are given in Grzybowski (1980).

Habitat height (HHT) and habitat density (HDEN) represent the primary habitat gradients present in the grasslands studied (Grzybowski 1980). Vegetation height for a 15-m^2 block was the average of four point samples about 1 m apart, and measured to the nearest centimeter. HDEN is:

$$\mathrm{HDEN} = \sum_{m=1}^{4} \sum_{k=1}^{25} x_{km} \tag{1}$$

where x_{km} is the number of vegetation contacts made with the tip of a wire passed through the vegetation for 30 cm at the kth height (at 10-cm intervals from 5–245 cm), and mth point (of four).

Habitat preferences were determined in the 1975–76 and 1976–77 seasons for each species on each specific grazing treatment (Grzybowski 1980). Strips 1000 × 60 m were established on each site, and these divided into 15-m^2 blocks. Frequency occurrence of bird species in the blocks was recorded during visits to each treatment type. The habitat values for a species on a given site were determined by averaging the HHTs and HDENs of blocks in which the species was observed. Each block used by a bird species was weighted by the frequency occurrence of that species in the block. Additional habitat sampling was conducted to characterize Horned Lark (see Table 1 for scientific names) and Chestnut-collared Longspur habitats on a HG in western Texas during the 1977–78 and 1978–79 seasons. Thirty samples, measured as above, were obtained at locations from which these species were flushed, and averaged to provide values of the habitats used.

Maps were created for five Oklahoma, two southern Texas and two western Texas sites. Flushing and landing points of birds were recorded on site maps to document space use. These points were plotted by triangulation with a single row of stakes marking the grid-blocks or with other landmarks. Only observations made on the first pass through a site were used to avoid recording space use affected by the observer.

Individual distance (IDIS) was used as a measure of spacing. The IDIS was estimated for pairs of individuals encountered on the ground or recently flushed: (a) in body lengths for distances less than 1.5 m; (b) to the nearest 0.5 m for distances less than 5 m; and (c) to the nearest meter for distances greater than 5 m. The distances to the nearest individual were obtained through direct observation or by walking spirally around the bird's flush point to 25 m (or more in a few cases) until another individual was encountered. When the nearest individual was not a conspecific, the distance to the nearest conspecific was also obtained.

Distinctions were made in western Texas among HGs grazed by cattle and those grazed primarily by prairie dogs (*Cynomys* sp.; PD). Observations made in January 1979 were separated from those made in the 1976–77 through 1977–78 seasons for a HG in western Texas; the site was ungrazed in 1978 and was in its initial stages of recovery in January 1979. Also, in January 1977, densities of LeConte's Sparrows on a LG in southern Texas were seven times higher than the next highest estimate (Grzybowski 1982) and far above what previous investigators had encountered (Emlen 1972; G. Blacklock, pers. comm.). Observations of LeConte's Sparrows on this site were separated from the others for analysis.

RESULTS

Mean values of IDIS, HHT, and HDEN for each species by grazing treatment and region are given in Table 1. Simple correlation coefficients of IDIS with HDEN and HHT were significant ($r = 0.57$, $P < 0.05$). Horned Larks and Lapland Longpsurs, which occupied the most open habitats, maintained mean individual distances of 2 m or less. Other gregarious species such as Chestnut-collared and Smith's longspurs and Vesper Sparrow, which occurred in habitats with intermediate cover values, maintained mean individual distances of 3–8 m (exceptionally 12.7 m). For most grassland sparrows, however, mean IDIS was normally greater than 11 m, and in entirely solitary species, was greater than 17 m. These sparrows most often occurred in the habitats with the highest cover values.

Space-use patterns exhibited by grassland birds are summarized in Fig. 1. Each square represents an area which is large relative to the individual bird. Space-use patterns vary from those of the LeConte's Sparrow (Type 1), where individuals appear territorial, to those of species like Lapland Longspurs (Type 4b), where individuals use large continuous areas, but where the distribution of individuals at any time is highly clumped. Patchy use of grassland habitats is exhibited by gregarious species (Type 4a) and solitary species (Type 2b). Each type is discussed below.

LeConte's Sparrows were solitary. On a LG in central Oklahoma, they could regularly and predictably be located within particular 15-m-blocks. Their locations, made from plots of their flush routes taken from December 1975 through February 1976, strongly implicate active spacing mechanisms, and perhaps territoriality. On one southern Texas site which supported a very high density of LeConte's Sparrows, spacing patterns were so regular in some patches that as many as 12–17 different birds (three occasions) were flushed, one every five to seven steps.

Baird's and Grasshopper sparrows were also solitary on LGs in western and southern Texas, respectively, and exhibited spacing patterns of type 2a (Fig. 1). Distances flushed by Baird's Sparrows were more than triple those for other solitary species (unpubl.). Of 14 initial flushes of Baird's Sparrows, three birds flew to landing positions beyond the resolution of the observer watching with 7 × 35 binoculars. On one occasion, a Baird's Sparrow landed within 5 m of a second sparrow. Both flushed in opposite

TABLE 1
MEAN VALUES OF INDIVIDUAL DISTANCE AND HABITAT DENSITY AND HEIGHT FOR GRASSLAND BIRD SPECIES BY REGION AND TREATMENT

Species	Treat-ment[a]	Region[b]	Individual distance	Habitat density	Habitat height
Horned Lark	CU	Okla	1.7	0.8	0.8
(*Eremophila alpestris*)	LG	WTex	1.8	30.8	21.6
	HG	WTex	2.2	10.0	7.5
	PD	WTex	1.6	4.5	3.5
Savannah Sparrow	LG	Okla	13.2	47.5	45.1
(*Passerculus sandwichensis*)	MG	Okla	100.0	32.3	40.6
	HG	Okla	18.7	38.6	23.8
	LG	STex	6.9	52.0	60.1
	MG	STex	14.1	52.0	60.1
	HG	STex	12.2	28.4	23.3
Grasshopper Sparrow (*Ammodramus savannarum*)	MG	STex	19.5	68.8	63.6
Baird's Sparrow (*Ammodramus bairdii*)	LG	WTex	60.7	30.0	21.6
LeConte's Sparrow	LG	Okla	42.7	66.4	63.2
(*Ammodramus leconteii*)	LG	STex	11.1	—	—
	MG	STex	17.1	64.0	63.2
Vesper Sparrow (*Pooecetes gramineus*)	MG	STex	3.7	37.7	24.6
Lapland Longspur (*Calcarius lapponicus*)	CU	Okla	1.5	0.6	1.0
Smith's Longspur	MG	Okla	2.9	33.5	39.0
(*Calcarius pictus*)	HG	Okla	2.9	37.7	21.2
Chestnut-collared Longspur	MG	Okla	5.4	29.3	38.7
(*Calcarius ornatus*)	HG	Okla	6.5	25.5	17.3
	HG	WTex	12.7	15.5	14.5
	HG[c]	WTex	7.6	17.6	14.5

[a] CU = cultivated; HG = heavily grazed; LG = lightly grazed; MG = moderately grazed; PD = prairie dog town.
[b] Okla = Oklahoma; STex = southern Texas; WTex = western Texas.
[c] Means from January 1979 when the site was recovering from being heavily grazed.

directions as was the case with LeConte's and Grasshopper sparrows flushed from adjacent locations.

Savannah Sparrows were variable in the use of space. They exhibited type 2b spacing patterns (Fig. 1) on a LG in central Oklahoma where distinct patches with lower vegetation height and density than the site means (Fig. 2) were regularly used. Only one bird/patch occurred in the smallest patches. Birds in patches occupied by more than one individual were normally solitary, but flew near each other when disturbed. On MGs in Oklahoma, where patchiness of habitat was not distinctive, birds exhibited type 2a spacing patterns similar to Baird's Sparrows in western Texas.

On some sites, where Savannah Sparrow densities were high, the type 3 spacing pattern (Fig. 1) was observed. Savannah Sparrows were widely spaced when first encountered with mean inter-individual distances of 7–14 m (Table 1), but often joined in groups when disturbed. These groups would continue to grow in numbers as I progressively chased birds about the area and would travel circular paths within certain bounds. Fig. 3 shows areas occupied by groups of sparrows on an Oklahoma site. On a southern Texas site where densities were very high, the paths of groups overlapped and could not clearly be defined. These groups may have been composed of different combinations of individuals for each observation, their composition dependent on the path of movement of the observer.

On one Oklahoma site, about 30 Savannah Sparrows, which formed into a group when disturbed by the observer, could be chased to the edge of their cover, where they circled back and dispersed as solitary birds. A repeat performance occurred in 0.5 h, when all birds were dispersed singly. Basically, Savannah Sparrows on this site maintained solitary behavior except when disturbed.

Smith's and Chestnut-collared longspurs were gregarious but frequented specific patches of a grassland site (Type 4a; Fig. 1). Use by Smith's Longspurs on a HG in central Oklahoma appeared to favor particular patches with vegetation heights lower than the site mean (Fig. 4A) but with moderate to low vegetation densities (Fig. 4B). These patches generally contained dense growth of three-awn (*Aristida* sp.), a short flimsy grass species, and silver beardgrass (*Andropogon saccharoides*). Chestnut-collared Longspurs occurred mostly in pockets of sparser, but similar vegetation (Fig. 4A, B) between areas used by Smith's Longspurs. Smith's Longspurs, observed on two sites, also favored dense patches of three-awn and silver beardgrass (pers. obs.). Chestnut-collared Longspurs observed on MGs, where no other longspur species occurred, used particular areas extensively during one winter season (unpubl.).

Lapland Longspurs and Horned Larks exhibited type 4b spacing patterns (Fig. 1). Lapland Longspurs on most cultivated sites in central Oklahoma, and Horned Larks on a prairie dog town in western Texas occupied extensive and continuous areas of their site. However, at any one time their distributions were clumped. They were often observed flying overhead from most grassland sites, and often from non-grassland sites in loosely spaced groups.

In western Texas during two years of the study, Chestnut-collared Longspurs exhibited type 2c spacing pattern (Fig. 1). Birds were widely scattered during the day (08:30–16:00). One very widely spaced group of 16

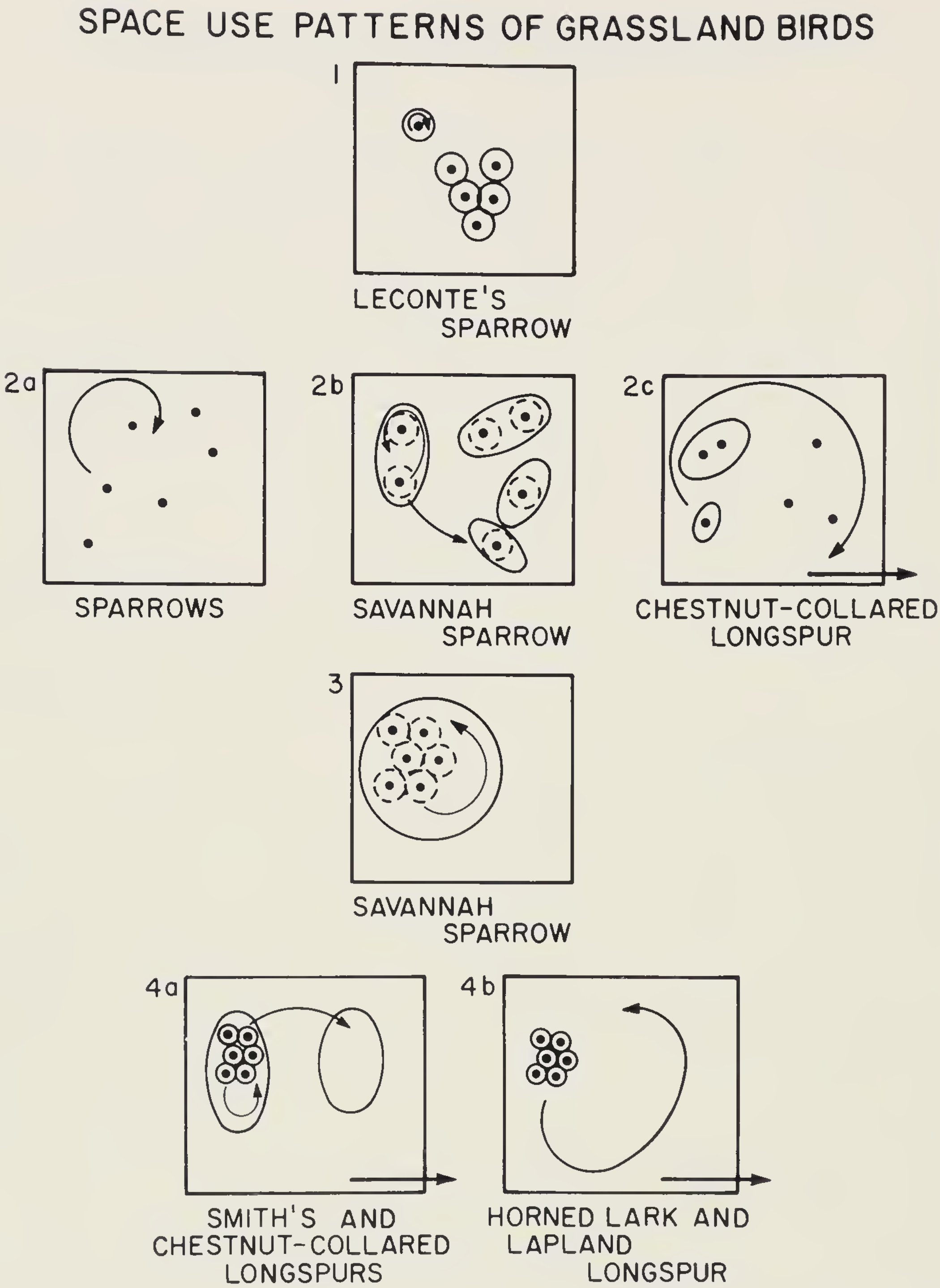

FIG. 1. Diagramatic representation of spacing patterns exhibited by grassland birds during winter. Four types are identified. Each square represents an area which is large relative to the individuals. Individuals are represented by dots; six dots in each square are used for convenience. Solid circles surrounding dots in type 1 represent use-areas to which enclosed individuals (dots) restrict themselves. Circles formed with dashed lines represent temporary use areas. Three sizes of circles are used—the smallest for types 4a and 4b represent areas of individual distance; intermediate in types 1, 2b, and 3 represent "territories" or individual spacing units larger than individual distances; and the largest for type 3 represents an area of group activity. Ellipses (in types 2b and 4a) represent patches of preferred habitat. Arrows depict the magnitude of potential movements by individuals, including within "territories"

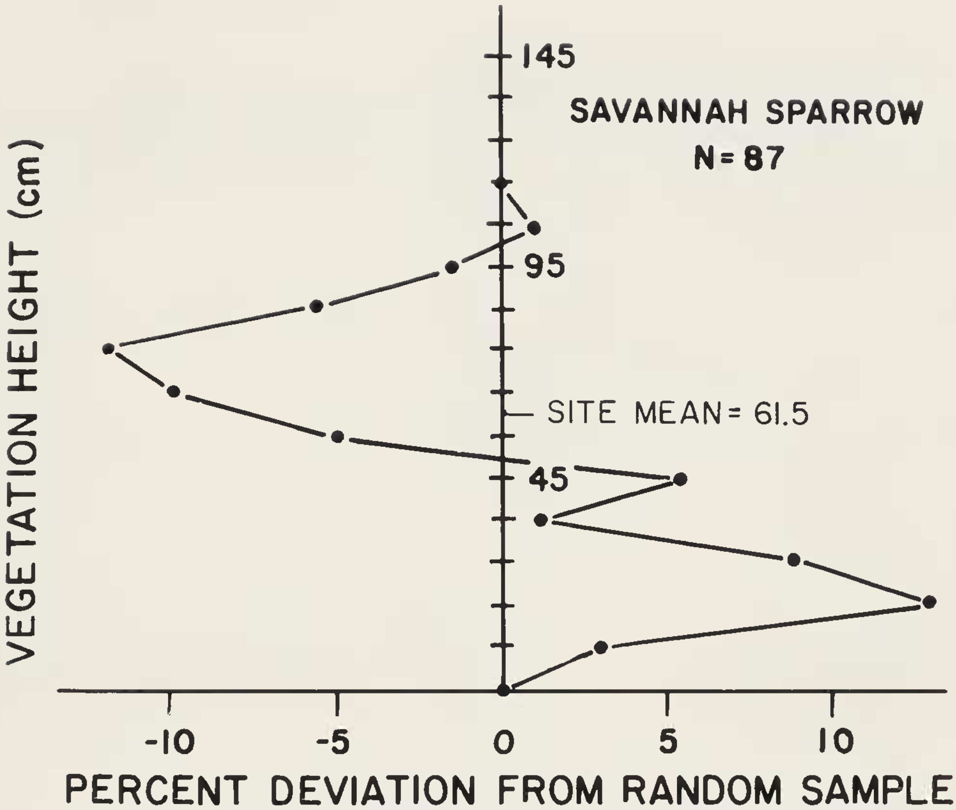

FIG. 2. Distribution of vegetation heights used by Savannah Sparrows as they deviate from the distribution of a random sample on a lightly grazed grassland in central Oklahoma during the winter of 1975–76. Mean vegetation height is 61.5 cm.

was located (in 19 days of observation), in addition to other groups of 5, 7, and 11 individuals. All other observations were of one or two birds. Seed abundance was low compared to other sites (Grzybowski 1982, 1983), and may account for the solitary foraging behavior of these birds. In January 1979, one or two groups of Chestnut-collared Longspurs (numbering from 18–30) were located on a heavily grazed site in patches where three-awn was conspicuous; they exhibited type 4a spacing patterns (Fig. 1). Seed density was also higher in these patches than in other areas where single birds occurred (Grzybowski 1982, 1983).

DISCUSSION

Passerines occupying grasslands exhibit territorial defense in spacing themselves during the breeding season (Cody 1968, Murray 1969, Wiens

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(type 1), locally within site (type 2a), within and between patches (types 2b and 4a), within group activity areas (type 3), within site (types 2c and 4b), and between sites (types 2c, 4a, and 4b).

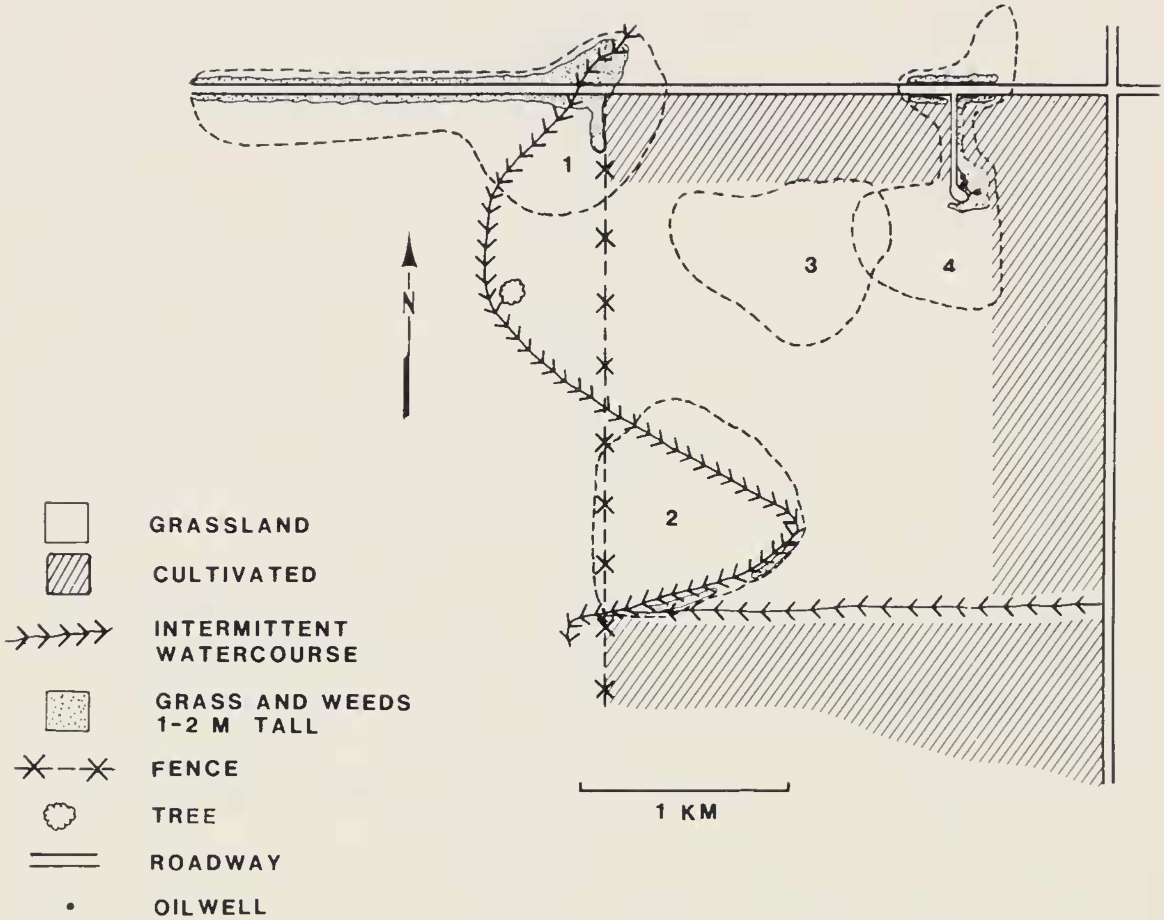

FIG. 3. Space use by groups of Savannah Sparrows (delimited by dashed lines) on a successional grassland in central Oklahoma during the winter of 1977–78. (See text.)

1969). In winter, only LeConte's Sparrows in Oklahoma exhibited spacing patterns resembling territories; but this spacing behavior may be the result of avoidance rather than active defense. However, evidence is indirect. Many individuals on a southern Texas site, when bird densities were extremely high, were uniformly spaced about 6 m apart. In addition, grasslands used by LeConte's Sparrows were often seed-poor (Grzybowski 1982, 1983); defense of areas on these sites may cost more in energy than the resource base can support. Leconte's Sparrows may need to conserve energy just to occupy these grasslands. Crops of LeConte's Sparrows collected in southern Texas rarely contained more than 20 seeds, even at dusk, compared to 200 or more seeds in crops of Savannah Sparrows (unpubl.), further implicating the impact of low seed availability and energy conservation for LeConte's Sparrow.

Because avoidance behavior is a subtle process compared to overt aggression, it has been little studied. Waser (1976) found that groups of gray-cheeked mangabeys (*Cercocebus albigena*) avoided each other. East-

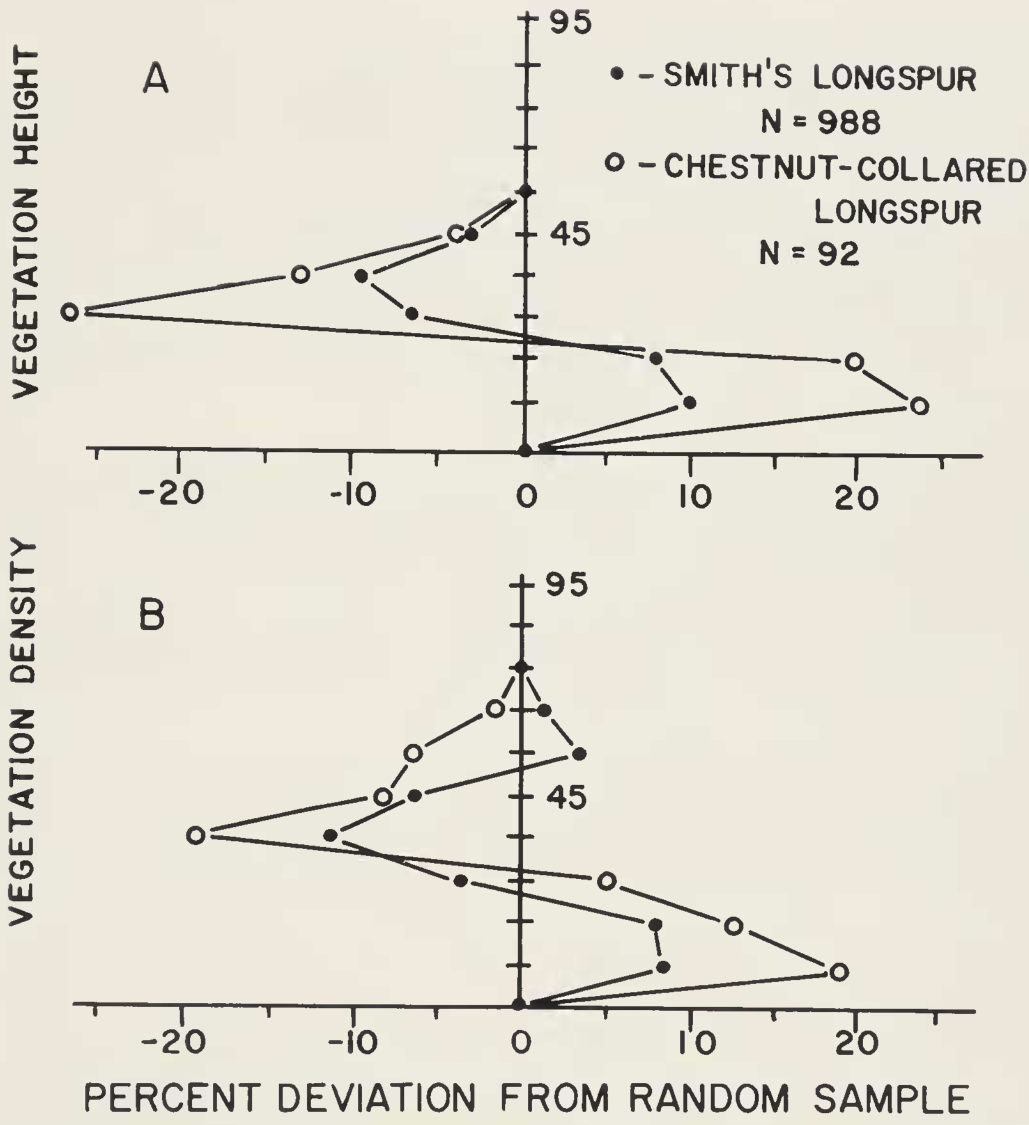

FIG. 4. Distributions of vegetation heights and vegetation densities (see text) used by Smith's and Chestnut-collared longspurs as they deviate from the distribution of a random sample on a heavily grazed grassland in central Oklahoma during the winter of 1975–76. Mean vegetation height is 26.2 cm; mean vegetation density is 29.7 vegetation contacts.

ern chipmunks (*Tamias striatus*) maintain overlapping territories defended from non-territorial intruders; however, established neighbors avoided encountering each other on overlapping portions of their territories (Getty 1981). In birds, this process has not been demonstrated.

More commonly, grassland birds were not as restrictive or exclusive in their use of space as LeConte's Sparrows. Species such as longspurs were highly gregarious and mobile (Grzybowski 1983). They occupy exposed grasslands with moderate to high seed densities. Gregariousness of longspurs in these habitats may serve in enhancing early predator detection (Caraco 1979). Gregarious species occurred in habitats with low or intermediate HDEN. Solitary passerines never occurred in sparsely vegetated grasslands.

Lapland Longspurs and Horned Larks occurred in the sparsest grassland habitats with almost no cover. Lapland Longspurs form large groups, and Horned Larks in November (pre-breeding) were primarily flockers. Chestnut-collared Longspurs observed in migration in plowed fields were also seen in large groups. Large flocks in open terrain may be useful in flocking maneuvers which evade avian predators or increase the predator's risk of collision with non-target birds (Treisman 1975). I observed Prairie Falcons (*Falco mexicanus*) attempting to capture these species on four occasions; the falcons flew low toward a flock. These longspurs and larks all flew up in response to a falcon, forming into a tight group. Horned Larks responded similarily to Burrowing Owls (*Athene cunicularia*) accidently flushed by the observer into the flocks.

The attraction of grassland birds to sites with higher seed densities may make it impossible for individuals to maintain territorial defense against intruders. Myers et al. (1979) observed this condition in Sanderlings (*Calidris alba*) using areas of high prey density. In open grasslands, the combination of exposure to predation, which clusters birds, exposure to weather, which increases energy demands, and the attraction of more individuals to sites with higher seed densities, creates a situation where seeds can be locally exploited. This may impose the need for a mobile and energetically more costly strategy, where groups look for patches or sites (which could be considered patches for larger groups) with seed densities high enough to support groups and compensate the energy requirements necessary to find the patches. This process of patch use may be a variation of risk-aversion flocking described by Caraco (1980) and mediated by the need of birds in exposed habitats to form groups which enhance predator detection and increase an individual's foraging time (Caraco 1979). These conditions may preclude territorial space use patterns for grassland birds during winter, and encourage intra- and intersite mobility.

A potential compromise between the advantages and disadvantages of flocking is found in Savannah Sparrows. At moderate to high bird densities, Savannah Sparrows clustered in only part of their habitat use area at any time (Fig. 1, Type 3), but were spaced apart at 12–14 m. The data of first-disturbed birds indicate that Savannah Sparrows have evolved spatial and social habits which take advantage of spacing birds apart, yet still have positive group effects. This may be a very flexible system in which sparrows use the level of disturbance by potential predators to adjust individual distance in such a way that the benefits of predator detection are enhanced while the costs of flocking are reduced.

Pulliam and Mills (1977) presented evidence that space use by grassland sparrows may be affected by the presence of tree or shrub cover. According to these authors, competing species vie for positions near cover to enhance predator avoidance. Pulliam and Mills (1977) claimed that Savannah Sparrows are displaced from tree or shrub cover by Vesper Sparrows. In Fig. 3, however, only two of the four group ranges of Savannah Sparrows included cover greater than 1 m tall, in spite of the presence of this cover nearby and the absence of other sparrow species. In general, Savannah Sparrows avoided habitats with vegetation heights greater than 1 m unless they were disturbed repeatedly.

SUMMARY

The use of space by grassland birds during winter is variable, but generally exhibits patterns which indicate high intra- and intersite mobility. Only the LeConte's Sparrow exhibited space use resembling territories, but these may be maintained by avoidance rather than defense. Individual distance was inversely correlated ($P < 0.05$) with habitat height and habitat density. Social behavior enhancing predator detection appears to be an important factor influencing the use of space by grassland birds.

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